



Turbid reefs moderate coral bleaching under climate-related temperature stress

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Abstract

Thermal-stress events that cause coral bleaching and mortality have recently increased in frequency and severity. Yet few studies have explored conditions that moderate coral bleaching. Given that high light and high ocean temperature together cause coral bleaching, we explore whether corals at turbid localities, with reduced light, are less likely to bleach during thermal-stress events than corals at other localities. We analyzed coral bleaching, temperature, and turbidity data from 3,694 sites worldwide with a Bayesian model and found that K_d490 , a measurement positively related to turbidity, between 0.080 and 0.127 reduced coral bleaching during thermal-stress events. Approximately 12% of the world's reefs exist within this “moderating turbidity” range, and 30% of reefs that have moderating turbidity are in the Coral Triangle. We suggest that these turbid nearshore environments may provide some refuge through climate change, but these reefs will need high conservation status to sustain them close to dense human populations.

KEYWORDS

climate change, climate change refugia, coral bleaching, coral reefs, ordinal regression, resilience, thermal stress, turbidity

1 | INTRODUCTION

Coral reefs provide coastal protection and other goods and services for millions of people globally. Yet, coral reefs have recently experienced an increase in the frequency and intensity of thermal-stress events that are associated with climate change (Hoegh-Guldberg et al., 2014; IPCC, 2013). These thermal-stress events lead to coral bleaching, which is the loss of pigment from coral endosymbionts, or in extreme cases result in the expulsion of coral symbionts (Gates, Baghdasarian, & Muscatine, 1992). Coral bleaching can lead to coral mortality, which causes changes in the composition of coral communities, changes in total coral cover, declines in structural reef complexity, and loss of habitat for reef fishes. While we know that high intensities of thermal stress cause coral bleaching (Hughes et al.,

2018), and that coral bleaching is spatially and temporally variable (Sully, Burkepile, Donovan, Hodgson, & van Woesik, 2019), we know little about other environmental conditions that reduce coral bleaching, particularly over large regional scales.

Corals vary in their tolerance to thermal stress (Loya et al., 2001), which can be a consequence of the types of endosymbionts within corals (LaJeunesse, Loh, & Trench, 2009) or of the thermal tolerance of the coral host (Baird, Bhagooli, Ralph, & Takahashi, 2009). Coral bleaching occurs under high temperature conditions, but only when there is high light (Takahashi, Nakamura, Sakamizu, van Woesik, & Yamasaki, 2004). Experimental studies show that high-light intensity initiates coral paling through photoinhibition (Iglesias-Prieto, Matta, Robins, & Trench, 1992; Lesser & Farrell, 2004; Warner, Fitt, & Schmidt, 1999). Photoinhibition occurs when the rate of light energy absorption

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exceeds the rate of light energy conversion to chemical energy (i.e., ATP and NADPH) for use in carbon fixation (Suggett & Smith, 2019; Takahashi & Murata, 2008). Chronic photoinhibition occurs when high light and high temperature uncouple photosynthetic electron transport from ATP synthesis (Gorbunov, Kolber, Lesser, & Falkowski, 2001), leading to the formation of radical oxygen species (Lesser, 2006, 2011; Roberty, Bailleul, Berne, Franck, & Cardol, 2014; Roberty, Fransolet, Cardol, Plumier, & Franck, 2015). These cascading events suppress the rate of repair of the photo-damaged light-harvesting reaction centers, further accelerating photoinhibition (Murata, Takahashi, Nishiyama, & Allakhverdiev, 2007). High light, therefore, induces photoinhibition, and high temperatures exacerbate that photoinhibition, culminating as coral bleaching. Several studies have shown that reducing incoming light on heated corals reduces photoinhibition (Iglesias-Prieto et al., 1992; Lesser, 2019; Takahashi et al., 2004).

The reciprocity between light and temperature may explain some field observations that show reduced bleaching of corals in turbid waters. For example, there was less bleaching on turbid nearshore reefs than on other reefs during thermal-stress events in Palau (van Woesik et al., 2012) and in Brazil (Teixeira et al., 2019). Similarly, *Acropora*, a coral genus that is highly susceptible to thermal stress (Loya et al., 2001), bleached extensively in clear-water sites during recent thermal-stress events on the Great Barrier Reef (Hughes, Kerry, & Simpson, 2017), but did not bleach in turbid sites (Morgan, Perry, Johnson, & Smithers, 2017). Therefore, based on the outcome of physiological experiments on corals and on several field studies, we hypothesize that turbidity, the opacity of water resulting from suspended particles, is likely to reduce incident light and therefore reduce coral bleaching during thermal-stress events.

Indeed, some studies have shown that turbidity moderates bleaching at a local scale (Teixeira et al., 2019; van Woesik et al., 2012), or have used turbidity and temperature to predict regional climate-change refuges (Cacciapaglia & van Woesik, 2016), but no studies have quantified the moderating effects of turbidity on reducing coral bleaching on a global scale. We examine the relationship between thermal stress and turbidity at a global scale at 3,694 sites, using 8,797 Reef Check surveys in 81 countries, from 2002 to 2017.

2 | MATERIALS AND METHODS

2.1 | Biological and environmental data

The coral bleaching data used in this study were derived from 3,694 sites using 8,797 Reef Check surveys in 81 countries, from 2002 to 2017 (Figure S1). The Reef Check dataset (reefcheck.org) was collected by scientists and trained citizen-scientists using a standardized protocol (Hodgson, 1999; Sully et al., 2019). The validity of the Reef Check dataset is well documented (Done et al., 2017), and the data have been used in several global analyses (Hodgson, 1999; Sully et al., 2019). In each survey, the percentage of the coral populations experiencing bleaching was recorded. The latitude–longitude coordinates and the date of each survey were also recorded, which allowed us to find the corresponding environmental and temperature variables at time of field survey from other datasets and combine them with the Reef Check data.

The extent of wave exposure of every study site was determined through manual examination of the latitude–longitude coordinates in Google Earth, examining island and reef geomorphology and aspect, and overlaying prevailing wind patterns. We used the global Coral Reef Temperature Anomaly Database (CoRTAD Version 6), which has a weekly resolution of ~4 km, from the National Oceanic and Atmospheric Administration (www.nodc.noaa.gov/sog/cortad/) to model sea surface temperature (SST).

To derive a measurement of turbidity, we used NASA's (National Aeronautics and Space Administration's) Earth Observing System Data and Information System (EOSDIS) Modis-Aqua satellite database, which has an ~4 km resolution beginning in mid-2002 through to December 2017 (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/Kd_490/; Figure 1; Figure S2). Turbidity was considered to be positively related to the diffuse attenuation coefficient of light at the 490 nm wavelength (K_d490), or the rate at which light at 490 nm is attenuated with depth (Office for Coastal Management, 2019). For example, a K_d490 value of 0.1 m^{-1} means that light intensity is reduced by one natural-log value within 10 m of water. High values of K_d490 , therefore, represent high attenuation and hence high turbidity. While other measurements

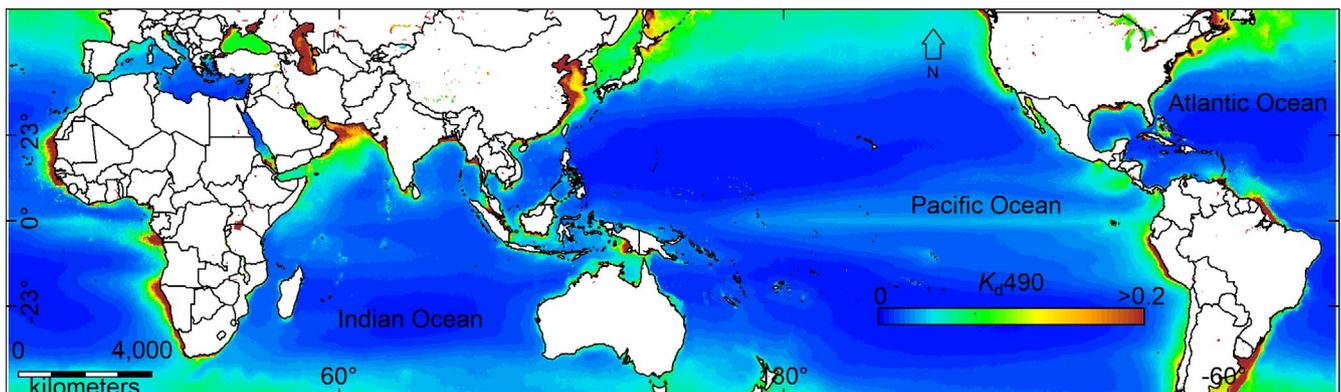


FIGURE 1 Global mean K_d490 values, indicative of turbidity, calculated monthly at a 4 km resolution

of turbidity, such as Nephelometric Turbidity Units or Formazin Turbidity Units, are more commonly used to describe turbidity, these data are typically only available using field sampling, and not available over a large scale, for example, from satellite data. K_d490 measurements are, however, directly related to the presence of scattering particles in the water column and are available globally at a 4 km resolution (Office for Coastal Management, 2019; Figure 1).

2.2 | Data analysis

A Bayesian hierarchical ordinal regression approach (Lunn, Jackson, Best, Thomas, & Spiegelhalter, 2012) was used to model coral bleaching and the effects of two environmental parameters (i.e., SST and turbidity) and their interactions on coral bleaching severity. Coral bleaching was measured as the percentage of the coral populations in each Reef Check survey experiencing bleaching, and was categorized into four levels: no bleaching, mild bleaching (1%–10%), moderate bleaching (>10%–50%), and severe bleaching (>50%; Figure S3). Notably, ordinal data are discrete data with a natural ordering, and in modeling we can generally assume they represent underlying continuous data (Lunn et al., 2012). The model incorporated standardized SST, turbidity, and the interaction of SST and turbidity. The following equations define the model system:

$$Y_i \sim \text{dcat}(p_{i,1:R}) \quad (1)$$

$$p_{i,1} = 1 - Q_{i,r-1} \quad (2a)$$

$$p_{i,r} = Q_{i,r-1} - Q_{i,r}, \quad \text{for } r \text{ in } 2 \text{ through } R-1 \quad (2b)$$

$$p_{i,R} = Q_{i,R-1} \quad (2c)$$

$$\begin{aligned} \text{logit}(Q_{i,r}) = & \gamma_1((X_{i,1} - \bar{X}_1)/\sigma_1) \\ & + \dots + \gamma_n((X_{i,n} - \bar{X}_n)/\sigma_n) \\ & - c_r + a_{i,s}, \quad \text{for } r \text{ in } 1 \text{ through } R-1 \end{aligned} \quad (3)$$

$$dc_i \sim \text{dunif}(0,100), \quad \text{for } i \text{ in } 1 \text{ through } R-1 \quad (4)$$

$$c_1 = dc_1 \quad (5)$$

$$c_i = c_{i-1} + dc, \quad \text{for } i \text{ in } 2 \text{ through } R-1 \quad (6)$$

$$a_s \sim \text{norm}(G_s, \tau) \quad (7)$$

$$G_e \sim \text{norm}(\mu, T), \quad (8)$$

where Y_i is the coral bleaching level for survey i on an ordinal scale, ranging from no bleaching to mild bleaching to moderate bleaching to severe bleaching; dcat is a categorical distribution, dunif is a uniform distribution; R is the number of bleaching categories (4 in this study); $p_{i,1:4}$ is the probability of survey i being in each of the four bleaching

categories; γ are coefficients; x are environmental covariates; σ are the standard deviations of the environmental covariates; n is the number of covariates; a are random effects of site (s), which hierarchically follow a normal distribution (norm) from the random effect (G) of ecoregion (e) with mean μ ; τ is variance across site; T is variance across ecoregion; $Q_{i,r}$ is the cumulative probability of having a score of r or more; c_r is a cut point for each category r ; dc , is the difference between the cut points (Lunn et al., 2012). The covariates were modeled with flat normal priors. The Bayesian hierarchical ordinal regression model was implemented in R and run through the “rjags” package (Plummer, 2019) that uses JAGS (Just Another Gibbs Sampler), with three chains, a burn-in of 4,000 and 5,000 iterations.

2.3 | Turbidity thresholds

Following the primary analysis above, we also sought to determine the values at which turbidity reduced bleaching severity. We fit gamma probability densities to the K_d490 frequencies for each level of bleaching (i.e., no bleaching, mild bleaching, moderate bleaching, and severe bleaching). The lower turbidity threshold, below which coral bleaching was not moderated, was defined as the K_d490 value at which the probability density of no bleaching to mild bleaching became greater than the probability density of moderate to severe bleaching. We used the likelihood ratio test (Equation 9) and a chi-square test to compare the model maximized over the entire parameter space with the different bleaching-level models.

$$\text{LR} = -2 * \ln(L_0/L_1), \quad (9)$$

where LR is the likelihood ratio, an assessment of the goodness-of-fit of two competing models, L_0 is the likelihood of the model maximized over the entire parameter space, and L_1 is the likelihood of the model with different bleaching levels.

We also sought to find the “breakpoint” where turbidity remains beneficial by reducing light stress on corals, but beyond which turbidity becomes detrimental because it deprives the corals of sufficient light for photosynthesis. To estimate this upper turbidity threshold, beyond which reef functionality is below optimum because of consistently low light (see Supplementary Document and Figure S4 in Supporting Information), we performed a case study along a turbidity gradient on the inner reefs of the Great Barrier Reef. At 42 islands along the turbidity gradient (Figures S5–S8), we gathered the K_d490 values from NASA's Earth Observing System Data and Information System (EOSDIS) Modis-Aqua satellite database, and we measured the width of the reef flats using Google Earth. We then fit a nonlinear least squares regression to the K_d490 values and the width of the reef flat. The K_d490 value at which the 95% confidence interval crossed zero was defined here as the upper turbidity threshold.

We also sought to identify the proportion of reefs in each marine ecoregion of the world that fell within the “moderating turbidity” threshold. Shapefiles of the coral reefs of the world overlaid with the turbidity values identified reefs that fell within the turbidity thresholds.

To partition the reefs of the world in accordance with marine ecoregions, shapefiles from ecoregions of the world (Veron, Stafford-Smith, DeVantier, & Turak, 2015) were overlaid with shapefiles of coral reefs of the world and the mean K_d490 raster file (Figure 1). For each marine ecoregion, we randomly sampled 10,000 points that fell within reef boundaries and determined the probability density of K_d490 values for reefs within each ecoregion. Additionally, we determined the total area (km^2) of reefs in each marine ecoregion that fell within the turbidity range where coral bleaching was moderated.

3 | RESULTS

The Bayesian hierarchical ordinal regression model showed that when considering the interaction between both elevated SSTs and turbidity, coral bleaching was reduced. By contrast, inputting either elevated SSTs or turbidity alone both increased the likelihood of coral bleaching (Figure 2).

The gamma model that treated the four bleaching levels separately (i.e., none, mild 1%–10%, moderate >10%–50%, and severe >50%) had a significantly ($p < .0001$) better fit than the null gamma model that was maximized over the entire parameter space (Figure 3). These results suggest that during thermal-stress events, coral bleaching was more likely on clear-water reefs than on turbid reefs.

The turbidity value at which water was too turbid for coral reef growth was found from performing a nonlinear least squares regression on a turbidity gradient in the inner Great Barrier Reef. The turbidity value at which the 95% confidence interval crossed zero was found to be 0.127 K_d490 . We use 0.127 K_d490 in this study only as an indicator of high turbidity where light is limiting, and are cautious applying this value too rigidly, across all coral reefs that vary in coral species composition (Figure S4). Globally, coral bleaching was reduced from moderate and severe bleaching levels to mild bleaching or no bleaching levels when K_d490 values were between 0.080 and 0.127.

Thirty-one percent of the “moderating turbidity” reefs worldwide were found in the Coral Triangle, including reefs in the Sulu Sea, the Banda Sea and Molucca Islands, the South-east Philippines, and Milne Bay Papua New Guinea ecoregions (Figure 4; Table S2). The Torres Strait and far northern Great Barrier Reef ecoregion also encompassed a large reef area (2,370 km^2) that experienced “moderating turbidity” (Figure 4; Table S2) on 18% of its coral reefs. Notably, 26% (688.64 km^2) of the coral reefs of the southern Red Sea ecoregion, and 25% (681.78 km^2) of the coral reefs of the Kenya and Tanzania ecoregion were located in the turbidity range that moderates coral bleaching.

4 | DISCUSSION

Our results show that “moderating turbidity” between 0.080 and 0.127 K_d490 can reduce coral bleaching during thermal-stress

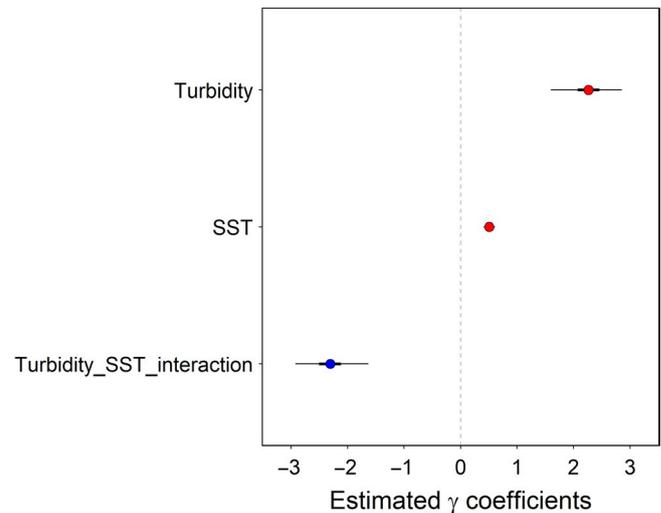


FIGURE 2 Ordinal regression model parameter coefficients showing the relationships between the four coral bleaching severity levels (i.e., none, mild 1%–10%, moderate >10%–50%, and severe >50%), and the two environmental variables (i.e., SSTs and turbidity) and their interaction within a Bayesian framework with mean values (circles) and 95% credible intervals (the thin black horizontal lines) as well as 50% credible intervals (the thick black horizontal lines) at 3,694 sites using 8,797 Reef Check surveys in 81 countries, from 2002 to 2017. SSTs are the sea-surface temperatures in $^{\circ}\text{C}$, and turbidity is measured as K_d490 values during the field survey period. Red dots show a positive relationship with bleaching severity, blue dots show a negative relationship with bleaching severity. All definitions are outlined in detail in Table S1

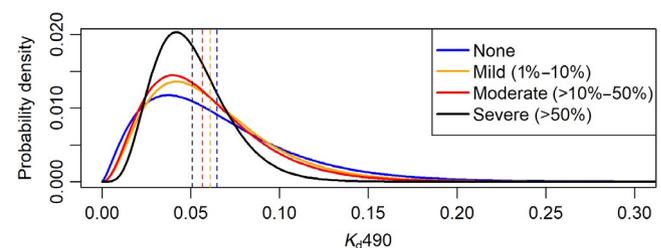


FIGURE 3 Gamma probability densities of K_d490 values (at 3,694 sites, using 8,797 Reef Check surveys in 81 countries, from 2002 to 2017), fit to data points from Reef Check surveys displaying no bleaching (blue), mild bleaching (orange; 1%–10% bleaching), moderate bleaching (red; >10%–50% bleaching) and severe bleaching (black; >50% bleaching). Dashed vertical lines indicate the mean K_d490 value for surveys in each bleaching category

events. These results agree with physiological experiments that show reducing light under thermal stress reduces bleaching by allowing the repair of the light-harvesting reaction centers in the endosymbionts (Takahashi et al., 2004). Our results also agree with recent field studies that observed reduced bleaching in turbid nearshore environments, even where temperatures were elevated (Morgan et al., 2017; Oxenford & Vallès, 2016; Teixeira et al., 2019; van Woësik et al., 2012). Interestingly, although the northern Great Barrier Reef was extensively bleached in 2016, reports showed

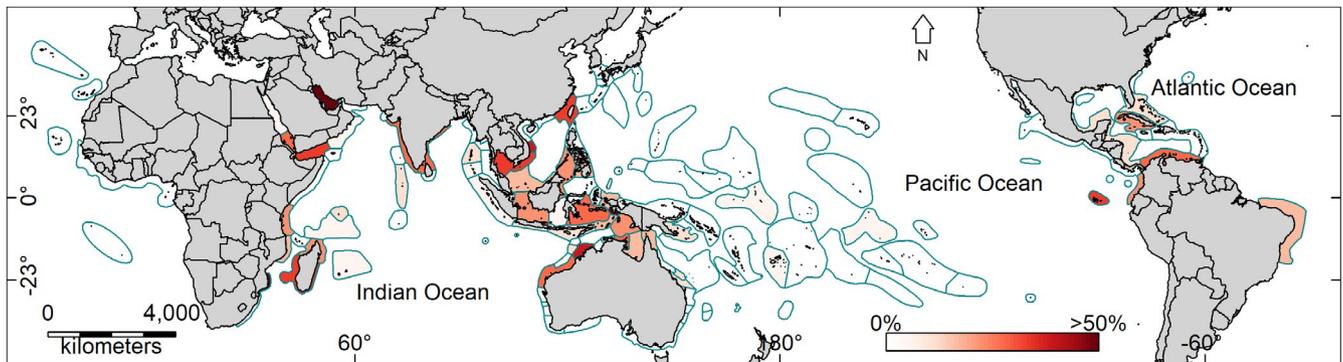


FIGURE 4 Percentage of coral reefs worldwide within the “moderating turbidity range” (of 0.080 – 0.127 K_d490) per marine ecoregion (which are outlined by fine blue lines). Data were obtained at 3,694 sites, using 8,797 Reef Check surveys in 81 countries, from 2002 to 2017

that chlorophyll-*a* concentrations, which effectively reduce light, were negatively related to coral bleaching, indicating that localities with high chlorophyll-*a* concentrations experienced reduced coral bleaching in comparison to localities with low chlorophyll-*a* concentrations (Hughes et al., 2017). In addition, *Acropora* corals, renowned for their thermal susceptibility, bleached extensively in clear Great Barrier Reef waters during thermal stress (Hughes et al., 2017), but did not bleach at turbid sites, which also experienced temperature stress (Morgan et al., 2017).

We selected a turbidity gradient along the inner Great Barrier Reef, between the latitudes 20 and 22°S, which has previously been shown to have long-term effects on lateral reef progradation (Kleypas, 1996). Extremely high and persistent turbidity through the past 5,000 years or more, a consequence of a 10 m semidiurnal tidal range at the head of Broad Sound, has prevented reef growth adjacent to Broad Sound (Kleypas, 1996), and has influenced coral composition, colony size, and coral-colony morphologies on modern reefs (van Woësik & Done, 1997). We used this gradient analysis to determine a potential turbidity threshold, beyond which reefs will be unable to grow (Kleypas, 1999). Although we fully acknowledge that regional thresholds will vary depending on coral community composition, we do expect a universal threshold of turbidity beyond which corals will not be able to function effectively.

Turbidity is most frequently considered detrimental to corals because of reduced light and tissue abrasion, with excess turbidity leading to a reduced euphotic zone (Kleypas, 1996) and reef shut-down under extreme conditions (Tomascik, Suharsono, & Mah, 1993). Yet, some turbid reefs fare well through thermal-stress events, and several coral species can feed on suspended particulate matter to derive carbon and nitrogen requirements (Anthony, 1999). Moreover, paleo studies suggest that reef corals spent considerable time in turbid environments through glacial periods (Potts & Jacobs, 2000), and glacial conditions prevailed through the Quaternary (Colinvaux, 1987; Lisiecki & Raymo, 2007). Therefore, turbid reefs, not clear-water oligotrophic reefs, may be the norm through history, as turbid environments were common habitats during sea-level and climatic fluctuations of the Quaternary (Potts & Jacobs, 2000). Our study suggests that turbid environments may continue to provide refuge for reef-building corals as the oceans warm.

Still, differential bleaching across habitats may not be simply a consequence of lower light conditions caused by turbidity, as nearshore corals may also support different symbionts than offshore corals (Fabricius, Mieog, Colin, Idip, & Oppen, 2004), and nearshore corals may be locally adapted to more extreme temperature conditions (Kenkel & Matz, 2016). In addition, not all kinds or causes of turbidity affect coral bleaching similarly. For example, turbidity can be seasonal, in the form of spring phytoplankton blooms (Bell & Tomascik, 1993) and river discharge events (Brown et al., 2017). While periodic turbidity may provide intermittent relief from thermal stress, episodes of high turbidity may be decoupled from the timing of thermal-stress events, and therefore provide no stable refuge for reef corals. By contrast, persistent turbidity, for example, turbidity driven by tidal forces over shallow habitats, continuously influences marine systems (Larcombe & Woolfe, 1999), and can do so for thousands of years (Kleypas, 1996; van Woësik & Done, 1997). Such persistent turbidity may indeed provide refuge for reef corals from climate-change induced thermal-stress events (Cacciapaglia & van Woësik, 2016).

In conclusion, the equatorial region in the Indo-Pacific Ocean has a third of coral reefs within the K_d490 range where turbidity may moderate coral bleaching (Figure 4; Table S2). This area known as the Coral Triangle is also the epicenter of marine biodiversity. We suggest that, as in the geological past, nearshore turbid reefs, not clear-water oligotrophic reefs, are most likely to provide refuge for corals through climate fluctuations. However, nearshore turbid reefs are also most vulnerable to local pollution and land-use change. Although less aesthetically appealing than clear-water oligotrophic reefs, nearshore turbid reefs will need particularly high conservation status not only because they are acting as modern climate-change refuges and are diversity repositories but also because they are close to human settlements. As climate change continues to threaten coral reefs globally, it is imperative to know where climate-change refuges are located. This knowledge can help policy makers and managers plan and adapt to perennial change by focusing conservation efforts and resource planning on localities that will likely survive through thermal-stress events, including many nearshore equatorial coral reefs.

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DATA AVAILABILITY STATEMENT

All the R code and Reef Check data for the analysis are available at the GitHub repository for the Institute for Global Ecology <https://github.com/InstituteForGlobalEcology/Turbid-reefs-moderate-coral-bleaching-under-climate-related-temperature-stress>. The Coral Reef Temperature Anomaly Database (CoRTAD) data used in this analysis are publicly available at NOAA's National Centers for Environmental Information (NCEI) webpage (<https://data.nodc.noaa.gov/cortad/Version6/>). K_d490 data are publicly available at the NASA, Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group, SeaWiFS (Sea-viewing Wide Field-of-view Sensor) Ocean Color Data webpage (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/Kd_490/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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